

Effect of salt stress on growth, lipid peroxidation and antioxidant enzymes in leaves and roots of maize (*Zea mays* L.)

N.Kh. Aliyeva

Laboratory of Cell Membrane Systems, Institute of Molecular Biology and Biotechnologies, Azerbaijan National Academy of Sciences, 11 Izzat Nabiyev, Baku AZ 1073, Azerbaijan

*For correspondence: enahide@rambler.ru

Some morphophysiological parameters, the content of malondialdehyde (MDA), which is a main product of lipid peroxidation, activities of the enzymes, superoxide dismutase (SOD), ascorbate peroxidase (APX) and guaiacol peroxidase (GPX) have been studied comparatively in maize plants (*Zea mays* L.) cultivated in the artificial climate chamber, at various concentrations of NaCl (1%, 2%, 3%). Based on the results of the study, the development of roots and leaf area is attenuated with increasing salt concentrations. The malondialdehyde content was found to increase with the rising NaCl concentration. At a 1% salt concentration, the SOD, APO, and GPO activities increased in maize roots and leaves compared with the control, whereas at 2-3% concentrations of NaCl the activities of the enzymes were partly inhibited.

Keywords: *Zea mays* L., salt stress, malondialdehyde, antioxidant enzymes, mesophyll cells, chloroplast, bundle sheath cells

INTRODUCTION

Maize plants (*Zea mays* L.) use C_4 photosynthetic pathway for the assimilation of CO_2 and this process is divided into two cycles. This division within the leaf is implemented by two specialized photosynthetic cells: mesophyll cells (M) surrounded bundle sheath cells (BS), located compactly around the veins. BS and M cells differ in their metabolic functions in the maize plant: PEP-carboxylase and C_4 photosynthesis function in M cells, whereas Ribulose-1,5-bisphosphate carboxylase (RBP) and Calvin cycle function in BS cells (Raines, 2003, von Caemmerer and Furbank, 2003). M cell chloroplasts of maize leaves have a granular structure and they possess all components of the electron transport chain, which ensures the photochemical functioning of PS I and PS II. In contrast, the granular structure is not clearly visible in BS cell chloroplasts where mainly PS I functions. Electron microscopy studies revealed differences between the structures of M and BS cells. Thus, M cells are characterized by granular structure, stromal thylakoids and small amounts of starch granules, whereas BS cells are

distinguished by their agranal structure and a greater amount of starch granules (von Caemmerer et al., 2003, Shao et al., 2015)

Abiotic stress factors, such as drought, salinity, flood, and extremely low temperature cause the disturbance of both photosynthetic and electron transport systems in plants (Allahverdiev et al., 1999). As a result, due to the decreased $NADPH^+$ in the Calvin cycle, the excess electrons are transferred to molecular oxygen O_2 , thereby forming reactive $O_2^{\cdot-}$ radical (Mehler reaction) (Tambussi et al., 2000). Although this radical is not directly harmful to radicals, it has an indirect effect as a source of H_2O_2 . Molecules surrounding $O_2^{\cdot-}$ radical binds two protons, forming hydrogen peroxide and O_2 . Hydrogen peroxide forms the harmful hydroxyl radical OH^{\cdot} , reacting with $O_2^{\cdot-}$ radical emerged in the presence of iron, copper and other transition metals (Haber-Weiss reaction) (Parvaiz et al., 2010; Jamei et al., 2009). These OH^{\cdot} radicals reacting with fatty acids form other harmful radicals (R^{\cdot} , ROO^{\cdot} , $RS^{\cdot-}$, etc.) (Yilmaz et al., 2011). Plants have various enzymatic and non-enzymatic defense systems protecting them from adverse effects of reactive oxygen species (ROS).

Antioxidants are considered to be substances existing at lower concentrations compared with oxidizing substrates. They are divided into 2 groups: enzymatic and non-enzymatic antioxidants and prevent or delay the oxidation of substrates. Non-enzymatic antioxidants include tocopherols, ascorbic acid, carotenoids, glutathione and phenolic compounds. Enzymatic antioxidants are superoxide dismutase, catalase, ascorbate peroxidase, glutathione peroxidase, glutathione reductase, glutathione S-transferase, glucose 6-phosphate dehydrogenase, etc. (Schafer et al., 2002; Arora et al., 2002).

Increased concentrations of ROS, such as superoxide radical, hydrogen peroxide, hydroxyl radical and alkoxy radical due to salt stress cause oxidative stress in plants. ROS produced in the cell are scavenged by the antioxidant defense system. Superoxide dismutase is one of the key enzymes converting $O_2^{\cdot-}$ radical into H_2O_2 with very high speed (Gajewska and Skłodowska 2007). Catalase and ascorbate peroxidase are enzymes playing the main role in the detoxification of H_2O_2 . Catalase converts H_2O_2 into water and oxygen. During the AsA-GSH cycle, ascorbate peroxidase (APX) uses ascorbate as a donor and prevents the formation of H_2O_2 (Ghasemi et al., 2013). Plants having a strong defense system better resist the effect of stressors (Parida and Das, 2005). The effect of ROS on plants depends on the neutralization degree of the antioxidant system (Demiral and Turkan, 2005; Khan and Panda, 2008).

One of the main indices of plant stress tolerance is malondialdehyde. Significant changes were found to occur in plant metabolic processes under the effect of various stress factors. One of these processes is lipid peroxidation. Malondialdehyde is accumulated in plant cells, due to lipid peroxidation under stress (Shao et al., 2005; Araujo et al., 2012; Hameed et al., 2015).

The SOD molecule was reported to have several isoforms— Cu/Zn-SOD, Mn-SOD and Fe-SOD—differing in the cellular localization, primary structure, molecule mass and the nature of the metals included in the active center (Alscher et al., 2002; Gill and Tuteja, 2010; Mahanty et al., 2012). Superoxide dismutase was detected in some organisms, including plants (Kumar et al., 2013). Contrary to SOD of animal cells, SOD of

plants is distinguished by numerous isoenzymes. Based on the previous reports, SOD activity changes under oxidative stress depending on the plant species, the stage of the plant development and the degree of the stressor effect (Alscher et al., 2002). Ascorbate peroxidases in the stroma of chloroplasts have four various forms: soluble peroxidase (sAPX), thylakoid-bound peroxidase (tAPX), cytosolic peroxidase (cAPX) and glyoxysomal membrane peroxidase (gmAPX) (Madhusudhan et al., 2003). APX is involved in the ascorbate-glutathione cycle and inhibits hydrogen peroxide using ascorbic acid as an electron donor. Guaiacol peroxidase is a heme-containing protein that oxidizes aromatic electron donors such as guaiacol and pyrogallol by H_2O_2 (Sharma et al., 2012). Guaiacol peroxidase is an antioxidant enzyme involved in numerous biosynthetic processes and playing an important role in plant protection from abiotic and biotic stresses (Erofeeva, 2015). GPX breaks down H_2O_2 by oxidation of auxiliary substrates such as phenolic compounds or ascorbate (Edwards et al., 1990).

The research focused on the effects of various concentrations of NaCl (1%, 2%, 3 %) on some morphophysiological parameters in vegetative organs of maize plants, the content of malondialdehyde (MDA), which is the main product of lipid peroxidation (LPO) in plant cells, and the activity of antioxidant enzymes (SOD, APO, and GPO).

MATERIALS AND METHODS

Object of the study: The maize plant (*Zea mays* L.) was cultivated in a phytotron in the soil (photoperiod – 14h/10h, temperature - 26°C/14°C, light intensity - 600 $\mu\text{mol m}^{-2}\text{s}^{-1}$). Salt stress was imposed by various salt concentrations (1%, 2%, 3%) upon the complete maturation of the second leaf using the available method (Hasan et al., 2005).

The effect of salt stress on growth parameters of the plant: The growth of the maize plants was controlled for 18 days. Then the lengths of roots and leaves were measured and fresh biomass was weighed (Saddige et al., 2016). The lengths of the stem, leaf and also the leaf area

were measured immediately after collecting samples.

The Leaf area: The Leaf area was determined following the formula of Carleton and Foote (1965):

$$\text{Leaf area (cm}^2\text{)} = \text{maximum leaf length} \times \text{maximum leaf width} \times 0.75$$

where, 0.75 is correction factor.

Phytotoxicity of root and leaf:

Phytotoxic effect of salt on the growth of roots and leaves was determined for 18-day-old plants using the following formula (Chou & Lin.,1976).

$$\text{Phytotoxicity of root/leaf (\%)} = \frac{L_c - L_T}{L_T} \times 100$$

where, L_c – root/leaf length in control; L_T – root/leaf length in treatment.

Tolerance index of root and leaf: The salt-tolerance of the maize plant was estimated by Wilkinson tolerance index (WTI) (Koornneef et al., 1997):

$$I_t = (I_m/I_c) \times 100$$

I_m – an increase in the root/leaf length caused by NaCl; I_c – an increase in the root/leaf length after 18 days.

Determination of the malondialdehyde content. The main product of the lipid peroxidation in plant tissues-MDA was determined based on the reaction with thiobarbituric acid (TBT) (Hatch and Osmond, 1976). 1 g of the plant material was homogenized after adding 20 ml of 0.1% (weight/volume) 3-chloroacetic acid. The homogenate was centrifuged for 10 min, at 12,000g. Then 4 ml of 3-chloroacetic acid (20%) containing 0.5% TBT was added to the supernatant and the obtained mixture was kept in the water bath for 30 min, at 95°C and cooled using ice. The optical density of the supernatant was determined by the spectrophotometer ($\lambda=532$ and 600 nm) after the repeat centrifugation for 10 min, at 12,000g. The MDA content was calculated using an extinction coefficient of 155 (nmol/g⁻¹ fresh weight) with the subtraction of non-specific absorption at 600 nm.

Extract preparation for enzyme assays: Lyophilized leaf (0.20 g) and root (0.15 g) powders were homogenized using a mortar and pestle with 4 mL of the ice-cold extraction buffer (100 mM potassium phosphate buffer, pH 7.0, 0.1

mM EDTA). The homogenate was filtered through a muslin cloth and centrifuged at 16,000 × g for 15 min. The supernatant fraction was used as a crude extract for the enzyme activity and lipid peroxidation assays. All operations were carried out at 4°C.

Superoxide dismutase (SOD, EC 1.15.1.1)

assay: The enzyme activity was determined at 450 nm using SOD Assay Kit (Sigma, Aldrich).

Ascorbate peroxidase (APX, EC 1.11.1.11)

assay: The activity of the enzyme was determined spectrophotometrically based on the decomposition of H₂O₂ by the ascorbate peroxidase enzyme for 1 min, at 290 nm (Nakano and Asada, 1981). The reaction medium consists of 0.1 mM EDTA (pH 8.0), 0.05 mM ascorbic acid, 0.1 mM H₂O₂, 50 mM Na-Phosphate (pH 7.6) buffer and 100 µl of the enzymatic extract. The APX activity was estimated based on the decline in the optic density during the first 30 sec of the reaction and was expressed in mmol ascorbate/(mg protein min) at the extinction coefficient (ϵ) of 2.8 mM⁻¹cm⁻¹.

Guaiacol peroxidase (GPX, EC 1.11.1.7)

assay: The total GPX activity was determined as described by Urbanek et al. (1991) in a reaction mixture (2.0 mL) containing 100 mM phosphate buffer (pH7.0), 0.1 M EDTA, 5.0 mM guaiacol, 15.0 mM H₂O₂ and 50µl of the enzyme extract. The addition of the enzyme extract started the reaction and the increase in absorbance was recorded at 470 nm for 1 min. The enzyme activity was quantified by the amount of tetraguaiacol formed using its molar extinction coefficient (26.6 mM⁻¹ cm⁻¹). The results were expressed as mol H₂O₂ min⁻¹ g⁻¹ DM taking into consideration that 4 mol H₂O₂ are reduced to produce 1 mol tetraguaiacol (Plewa et al., 1991).

Statistical analysis was performed in 3 biological replicates using the computer program Excel 2016.

RESULTS AND DISCUSSION

Maize seedlings exposed to salt stress for five days by various salt concentrations (1%, 2%, 3%) after the complete maturation of the second leaf were used in the experiments (Figure 1).



Fig. 1. Maize seedlings exposed to various salt concentrations (NaCl 1, 2, 3 %)

The response of roots to salt stress shows the salt tolerance potential of plants. The amount of O_2 decreases at high NaCl concentrations leading to a decline in the respiration rate and the plant loses its primary energy source. A high amount of ethylene is accumulated in plants, which impedes the root development (Koning & Jakson, 1979). The root growth was shown to be sensitive to high salt concentrations and a marked attenuation was observed in the root growth under high salinity (Mohammad et al., 1998; Cramer et al., 1988; Ashraf et al., 2005). We observed a pronounced decrease in the root length with increasing NaCl concentrations. Sizes of the maize plants also decreased significantly under salt stress. Thus, at high concentrations (2 and 3 %) of NaCl, the length of leaves and leaf area decreased sharply (Fig 2).

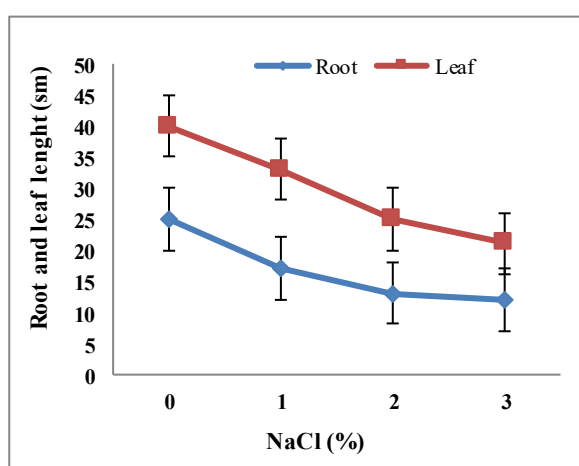


Fig. 2. Effect of salt stress on the root and leaf growth of *Zea mays* L. under different salt (0, 1, 2, 3%) concentrations.

Salt stress negatively affected the development of the leaf area in maize plants. A sharp decrease in the leaf area was observed with increasing (3%) salt concentrations (Figure 3).

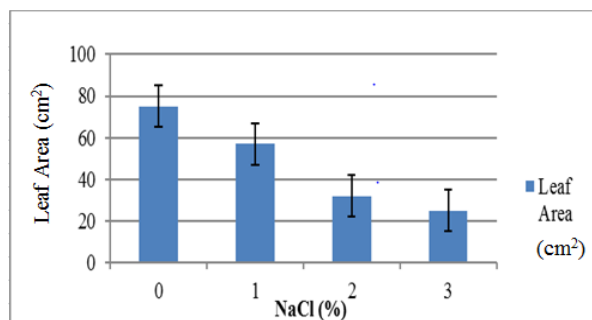


Fig. 3. Leaf area of *Zea mays* L. under salt stress.

Salt stress has a strong phytotoxic effect on the development of roots and leaves at high salt concentrations (2% and 3 %). This negative effect of NaCl is presented in Figure 4. The development of maize roots decreased significantly (especially at 2-3% NaCl) compared with the control with increasing salt concentrations. Our results are consistent with previous reports (Mahammad et al., 1998).

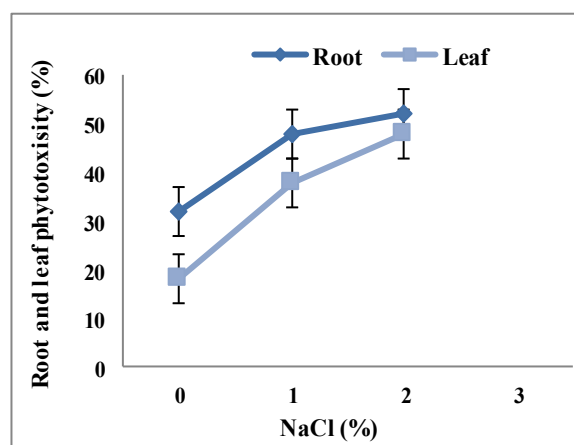


Fig. 4. Effect of NaCl concentrations on phytotoxicity of roots and leaves (%) in *Z. mays* L.

The increasing salt concentrations negatively affected the tolerance index of the plant. Maize plants exposed to 1% NaCl appeared to be more tolerant compared with those exposed to 2 and 3% NaCl (Figure 5).

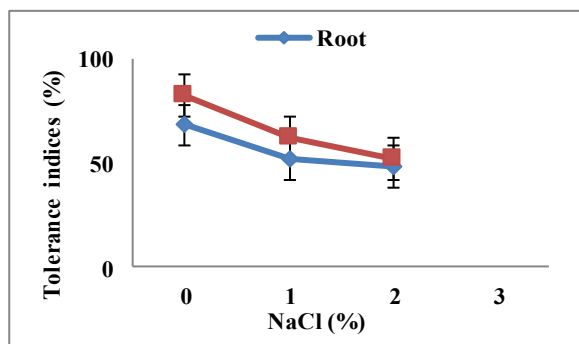


Fig. 5. Tolerance indices of maize root and leaf at different salt concentrations.

Table 1. Changes in the MDA content in leaves of the maize plants exposed to salt stress (nmol/g⁻¹ fresh weight)

NaCl	MDA content (nmol/g-1 FW)
0%	4.31±0.22
1 %	5.23±0.26
2 %	8.44±0.42
3%	11.91±0.59

Malondialdehyde is a product of peroxidation of unsaturated fatty acids in phospholipids and the level of lipid peroxidation is considered to be an indicator of the harmful effects of free radicals on cell membranes under salt stress. Therefore, MDA is assumed to be the main indicator of salt stress in various plants (Jain et al., 2001; Katsuhara et al., 2005; Jaleel et al., 2007). The MDA amount was found to increase in maize leaves and partially in roots with increasing NaCl concentrations (Hichem et al., 2009). The increase in lipid peroxidation under high salt concentrations (3%) is inhibited by exogenous salicylic acid. Salicylic acid prevents the accumulation of lipid peroxidation products.

At 1% concentration of NaCl, the SOD activity in roots and leaves increased significantly compared with the control and decreased with increasing salt concentrations. However, at a 3% concentration of NaCl, it remained at a higher level compared with the control (Table 2).

The APX activity changed markedly in leaves and roots of the maize plants with increasing salt concentrations. Thus, in roots, a positive correlation was observed between the salt concentration and the enzyme activity. Whereas, in leaves, the APX activity increased at 1% concentration of NaCl and decreased when the concentration was enhanced to 2% and 3%. The GPX activity increased with the rising salt concentration and at 3% NaCl the activity declined. In contrast, the enzyme activity decreased with the increasing salt concentration.

According to some authors (Amzallag et al., 1990; Djanaguiraman et al., 2006), the plant exposed to small concentrations of salt becomes tolerant to other stress factors. We also detected the adverse effects of high salt concentrations on the growth of the maize plants. Salt stress causes oxidative stress resulting in the activation of peroxidases, which play an important role in the defense against oxidative stress.

The accumulation of Na⁺ ions in roots and leaves is accompanied by the increase in the oxidative stress parameters, such as MDA and H₂O₂ amounts and the redox status of GSH and AsA was lowered in root tissues (Ashraf and Harris, 2004; Chawla et al., 2013). Due to the disorders in the electron transport chain occurred under stress, the ROS level increases in plant tissues resulting in the membrane damage (Pérez-López et al., 2009; Sharma et al., 2012). This excess of electrochemical energy is regulated by the Mehler reaction.

Our experiments showed that APX and GPX are the main antioxidant enzymes that neutralize H₂O₂ in both leaves and roots. The role of GPX in the elimination of H₂O₂ in the leaves and roots of maize is more important than that of APX. Thus, based on the obtained results and literature data, a significant role of the investigated enzymes in the disposal of the detrimental effects of ROS has been established (de Azevedo Neto., 2006).

Table 2. Activities of superoxide dismutase, ascorbate peroxidase and guaiacol peroxidase (μmol min⁻¹ mg⁻¹ protein) in roots and leaves of maize plants cultivated at various salt concentrations

NaCl	SOD		APX		GPX	
	Leaf	root	leaf	root	leaf	root
0%	39±0.02	22±0.04	0.53±0.018	1.12±0.008	0.05±0.02	3.28±0.003
1%	65±0.015	37±0.02	1.84±0.05	2.77±0.003	0.08±0.012	2.86±0.004
2%	55±0.018	29±0.03	1.05±0.009	4.28±0.002	0.57±0.008	1.3±0.007
3%	42±0.023	25±0.04	0.58±0.017	6.25±0.002	0.12±0.004	1.0±0.01

The results presented suggest that salt stress causes alterations in the metabolism of antioxidant substances in the roots and leaves of maize. Stress violates the balance between antioxidant reactions due to both osmotic and ion toxicity effects. At the same time, salt stress causes general metabolic disorders in the development of maize, which can lead to the destruction of the plant when the stressor is stronger.

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Duz stresinin qarğıdalı bitkisinin yarpaq və kökündə morfofizioloji parametrlərə, lipid peroksidləşmə və antioksidant fermentlərə təsirinin tədqiqi (*Zea mays* L.)

N.X. Əliyeva

AMEA Molekulyar Biologiya və Biotexnologiyalar İnstitutunun Hüceyrənin membran sistemləri laboratoriyası, Bakı, Azərbaycan

Təqdim olunan işdə NaCl duzunun müxtəlif qatılıqlarında (1%, 2%, 3%) suni iqlim kamerasında becərilən qarğıdalı bitkisinin (*Zea mays* L.) vegetativ orqanlarında bəzi morfo-fizioloji parametrlər, lipidlərin peroksidləşməsinin əsas məhsulu olan malondealdehydinin (MDA) miqdarı, superoksid dismutaza (SOD), askorbat peroksidaza (APO), qvayakol peroksidaza (QPO) fermentlərinin aktivlikləri müqayisəli öyrənilmişdir. Aparılan tədqiqatlar nəticəsində müəyyən olunmuşdur ki, duzun qatılığı artdıqca kökün uzunluğu və yarpaq ayasının ölçüsündə inkişaf zəifləyir. NaCl-un konsentrasiyası artıqca malondealdehydinin miqdarı artdığı müşahidə edilmişdir. Qarğıdalı bitkisinin kök və yarpaqlarında SOD, APO və GPO-nın aktivliyi kontrola nisbətən 1%-li stres zamanı artmış, lakin duzun 2 və 3%-li qatılığında fermentlərin fəallığı qismən inhibirlənmişdir.

Açar sözlər: *Zea mays* L., duz stressi, malondealdehydi, antioksidant fermentlər, mezofil, xloroplast, örtüktopa